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VISUAL ACUITY AND THE BALANCE BETWEEN RECEPTOR DENSITY AND GANG-ETC(U)  
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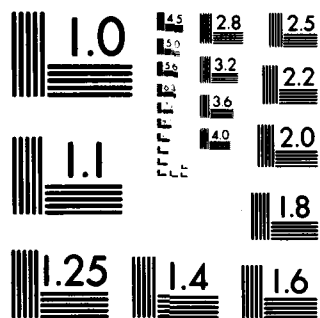
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VISUAL ACUITY AND THE BALANCE BETWEEN RECEPTOR DENSITY  
AND GANGLION CELL RECEPTIVE FIELD OVERLAP

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# ABSTRACT

Visual acuity has been analyzed in terms of the responses of the retinal ganglion cells to different stimuli within their receptive field. The analysis includes not only the relation of the response to the receptor matrix, but also to the neural processing within the retina. A discussion is given of the different methods of analyzing the receptive fields: sensitivity profiles and Ricco field (area x intensity) plots, and displacement sensitivity (the response to a small stimulus spot switched between two positions just touching each other). The difficulties with each of these methods of analyzing the receptive field are illustrated with experimental data. The experimental data also indicates that the blue cone system may not contribute to visual acuity, possibly due to the neural organization of the receptive field, rather than to the small number of blue receptors. The present data indicates that in the cat area centralis the average ganglion cell receptive field size is so large that through overlap, each retinal locus must be connected to at least 15 receptive field centers.

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## INTRODUCTION

The development of a theoretical basis to explain spatial vision has been very uneven. Many ideas that were arrived at from a theoretical basis have not held up under critical examination (e.g., the theory that high acuity resulted from eye movements panning an object). On the other hand, the components of spatial vision theory which have been the most helpful have been developed directly from experiments (e.g., lateral inhibition models). With this consideration in mind we have developed a theoretical framework based on known retinal anatomy and our measurements of ganglion cell receptive field properties.

Most theories of visual acuity ascribe the ultimate visual acuity attained to the relation of the retinal image size to the size of the photoreceptors in the retinal mosaic (e.g. Helmholtz, 1852; Stone, 1965; Green, 1970; Harter, 1970; Snyder, 1975). The details of the image on the retina are fine enough that the wave properties of light itself determine the intensity distribution. That is, an object so small or so distant in visual space that it is a point source from the standpoint of geometrical optics (a star, for example), is focused on the retina not as a point but rather as a diffraction-limited image (point spread function) (Gubisch, 1967). The details of the diffraction limited image are then dissected by the receptors.

The most important aspects of the retinal mosaic are the minimum center-to-center spacing of the receptors, their size, shape, and refractive index, all of which determine their waveguide properties (Snyder, 1975). The majority of the analyses of visual acuity in relation to the retinal mosaic have been concerned with how the retinal anatomy is matched to the image on the retina as calculated and measured with point spread functions. Models based on such analyses contain an implicit assumption that information transfer through the visual system presents a point-to-point topographical representation of the retinal receptor mosaic up to the cortical level. Thus, as an end result, each retinal receptor is represented in the cortex by a single cell or group of cells. In these models the responses of the cortical cell contain coded messages representing the intensity of the light on the appropriate receptor. However, the details now available of the anatomical structures in the visual system and the functions as presently known of any of the cells within the visual system are not compatible with a strict point-to-point representation for information transfer about location of images on the retina.

In non-primate vertebrates and in the extrafoveal regions of primate retinas, each ganglion cell must be connected to large numbers of receptors

since there are many times more receptors than ganglion cells. In the primate foveal region where the visual acuity is the best, the histological analysis of the retina suggests that there is nearly a one-to-one relationship between receptors and ganglion cells with, however, slightly fewer ganglion cells than receptors (Missotén, 1974).

In any model of the visual system which has point-to-point representation there must be as many ganglion cells as receptors and the connections between them must be simple. Evidence that a high degree of visual acuity can be attained without this sort of organization can be found in some animals. For example, in eagle and hawk eyes the optics and visual acuity are as good as in humans, if not better (Shlaer, 1972; Miller, 1976; Fox *et al.*, 1976). However, in the eagle and hawk foveas, the receptor to ganglion cell ratio is quite different from that in the human fovea. In both birds there are at least three and possibly ten receptors to one ganglion cell (Miller, 1976; Fite and Rosenfield-Wessels, 1972). This indicates that good visual acuity does not require as many ganglion cells as receptors. Furthermore, in these visual systems, at least, point-to-point representation of the receptor stage throughout the visual pathway cannot form the basis of visual acuity.

There is an additional consideration in computing the ratio of receptors to ganglion cells: ganglion cells are not all the same. They are not equivalent to each other in their function. On the basis of these differences in function they can be grouped into several distinct categories. For example, ganglion cells carry many different types of information in a sort of time sharing relationship. They carry the intensity information required for border contrast along with information about color contrast, for information can only leave the retina when it is funneled through the ganglion cells. This type of function dilutes the contribution to visual acuity. The net result is that the effective ratio of those ganglion cells which are responsible for acuity vision to receptors may be far less than is calculated from simple anatomical examinations which count all ganglion cells.

Within the visual system there are neural mechanisms which could act to increase contrast by amplifying small differences in intensity (Ratliff, 1965; Georgeson and Sullivan, 1975). This process could aid in spatial resolution by enhancing the contrast of borders in an image. It has been the purpose of this work to examine the basis for visual acuity, and especially to consider what role the organization of the neural system (that is, its anatomy and coding functions as now known) plays in determining the ultimate limit of visual acuity. It is possible that the distortion of the information by receptor to ganglion cell connections may form the fundamental and ultimate limit to visual acuity.

The whole problem of visual acuity is best understood, perhaps, by describing the various parts of the visual system beginning with the formation of an image on the retina. An examination of the receptor anatomy will be followed by a discussion of the connections of the receptors to the ganglion cells.

## Background

Every detection of light by the visual system may be divided into three stages. First, the light must pass through the optics of the eye and form an image on the receptor cells. Second, the receptor cells must absorb the light and transduce the light signal into an electric one. Third, the neural processing must detect and define the photo-receptor signals.

The limits of spatial resolution may be examined at each of these stages in turn, remembering that each stage acts on the signal which has been modified by the previous stage(s).

## Optical System

The essential features of the eye as an optical system are the cornea which provides most of the focusing power, the iris which provides a variable aperture and the lens which provides additional and adjustable focusing power. Because of imperfections in the optical structures, all eyes have a serious amount of spherical and chromatic aberration (LeGrand, 1967). Spherical aberration can be reduced by contraction of the pupil but a small pupil introduces another problem, and that is diffraction. Diffraction increases as the pupil size decreases while spherical aberration increases as pupil size increases. Figure 1 shows the intensity distribution of a point image on the retina with various pupil sizes. This figure illustrates the trade off between optical spread due to diffraction (the 1.5 mm pupil shows the greatest diffraction) and optical spread due to spherical and chromatic aberration (the 6.6 mm pupil shows the greatest spherical and chromatic aberration). The sharpest image is achieved with the pupil size in between the two extremes.

The point spread function provides a complete picture of the optical processing. The retinal image of an object can be constructed by adding the point spread function from all luminance points of the object (appropriately weighted for intensity), that is, by employing the principle of superposition. There is an equivalent and, in some cases, more convenient method of describing an optical system, and that is Fourier representation in the frequency domain. The familiar application of Fourier methods involves the conversion of time domain signals to the frequency domain. In this application any time varying signal can be represented by the sum of a number of appropriately weighted sine waves of different frequencies. Similarly, signals in the spatial domain (for example the Cartesian grid description of the luminance of some object) may be described in the frequency domain by the sum of a number of appropriately weighted sine waves. In this case, the sine waves are spatial. A spatial sine wave describes the sinusoidal undulation of luminance at a frequency of so many cycles per degree of vision.

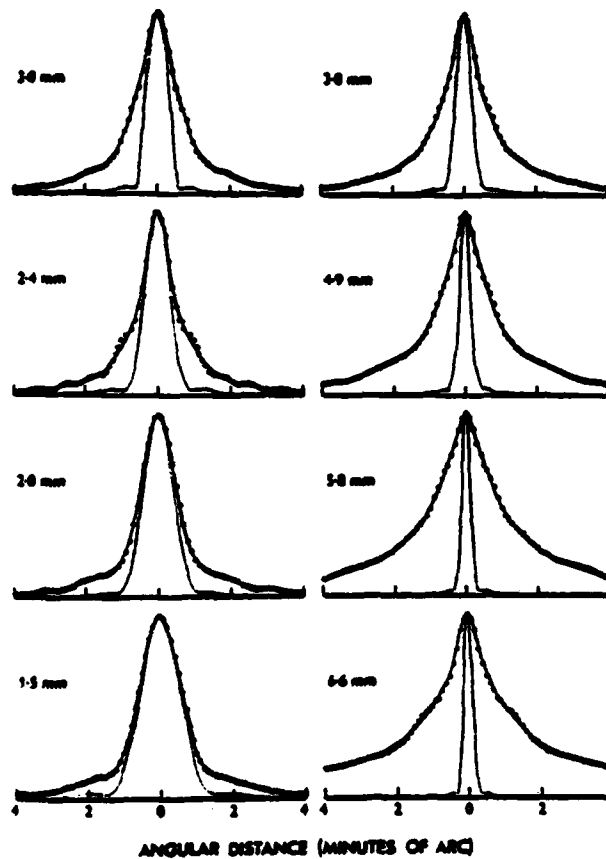


Figure 1: Optical spread functions for the human eye. Eight pupil diameters are shown varying from 1.5 mm to 6.6 mm. The heavy line is the profile of the retinal image. The thin line is the calculated optical spread due to diffraction alone (From Campbell and Gubisch, 1966).



For ease of description a simplifying assumption is generally used. That is, that visual performance and descriptions of visual parameters are similar in vertical and horizontal directions so all that is actually necessary is a one dimensional description. In the frequency domain the Modulation Transfer Function takes the place of the point spread. The Modulation Transfer Function (M.T.F.) describes the transfer of contrast through the optical system as a function of spatial frequency. This function is found by measuring the contrast reduction caused by passing a 100% contrast spatial sine wave grating (intensity =  $\sin(\omega x)$  where  $2\pi\omega$  = frequency (in cycles per degree) and  $x$  is distance (in degrees) along one spatial dimension) through the optical system, for a series of different frequency gratings.

The M.T.F. is the Fourier transform of the line spread function (similar to the point spread function except the object in this case is a line). As in any Fourier transform application, certain conditions must be met. First, the system must be linear, that is, if a sine wave is the input, the output must be a sine wave of the same frequency with a possible multiplication of the sine wave amplitude by a constant and a possible phase shift. Second, the system must be symmetric; that is, if only the axis of the input is changed then only the axis of the output will change (and to the same degree). Third, the system must be homogeneous; that is, it must show invariance to translation. These three requirements can all be met, at least locally, by the eye's optical system.

The M.T.F. of the human eye's optics is shown in Figure 2. The reduction in contrast for the high spatial frequencies is characteristic of any simple optical system and places a limit on visual acuity, a limit that the human visual system comes very near to achieving (Campbell and Green, 1965).

#### Receptor Stage

The receptor stage acts on the optically degraded image. In their turn the receptors also place a limit upon visual acuity. This limit is caused by the loss of any information about the light distribution upon a single receptor, since any one receptor only responds to the total light falling upon it. Any spatial detail (light and dark areas) in an image which will be preserved must involve the light and dark parts of the image falling upon different receptors. Therefore the receptor stage limits visual acuity to be no greater than the interreceptor distance.

The exact limit imposed by the receptor size will depend upon, among other things, the acuity test used (Westheimer, 1977). However, intuitive estimates are common. For example, Helmholtz (1866) believed that in order to identify two point sources of light as separate, the images of these sources must fall on two different receptors which are

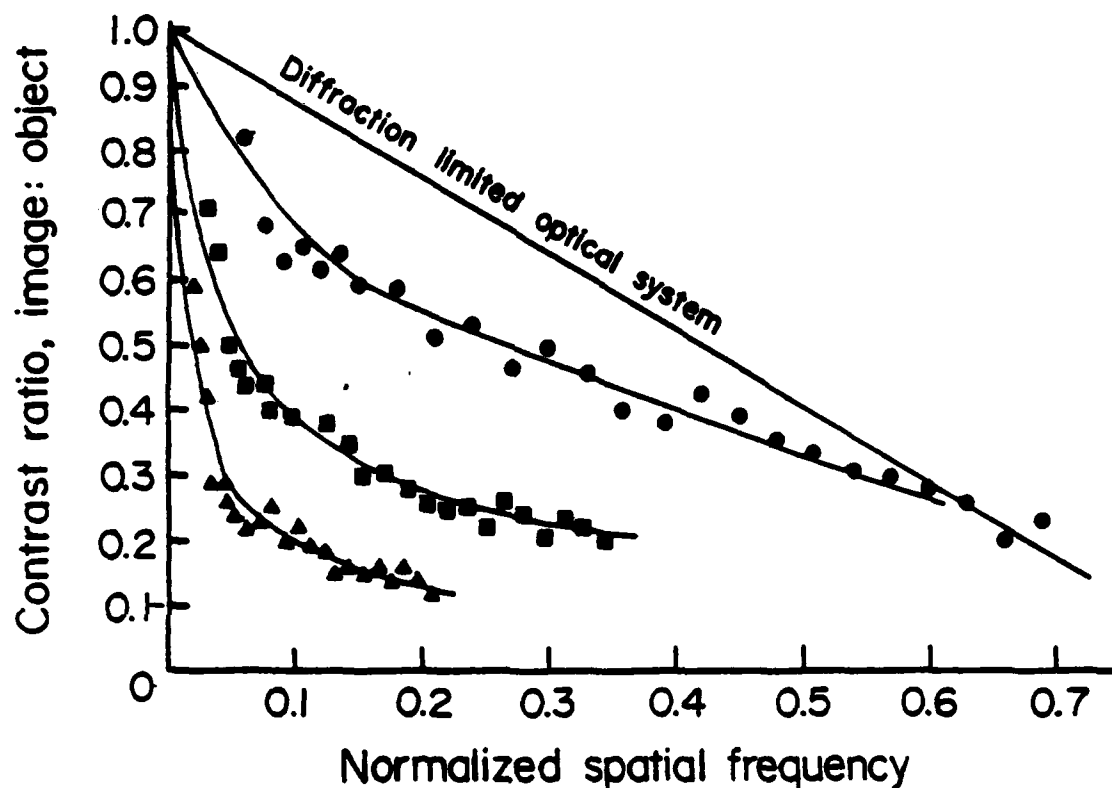


Figure 2: The modulation transfer function (M.T.F.) for the human optics. The data is obtained by presenting an eye with a 100% contrast spatial sinusoidal pattern varying in one dimension and measuring the contrast after it has passed through the optics (contrast is defined as  $L_{\max} - L_{\min} / L_{\max} + L_{\min}$ , where  $L_{\max}$  is the maximum luminance, the peak of the sine wave, and  $L_{\min}$  is the minimum luminance, the trough of the sine wave). The M.T.F. is the frequency domain equivalent of the spread function shown in Figure 1. High image to object contrast ratios correspond to thin spread functions (From Campbell and Green, 1965).

separated by at least one receptor which receives less light. A more modern and rigorous version of this comes from the Shannon-Nyquist sampling theory (Green, 1970). That theory states that the absolute minimum frequency of sampling must be twice the highest frequency in the signal in order to achieve unambiguous reception (Taub and Schilling, 1971). In application to the visual receptors, the Shannon-Nyquist theory says that the receptors (or samples) must occur at twice the density (or rate) as the changes in the image intensity (spatial frequency) which are to be resolved. Intuitively then, it seems that to increase acuity, all that is necessary is smaller (and more densely packed) receptors. However, there are two factors which would prevent receptors that are too small from operating efficiently.

The first is that the size of the receptors already approaches the wavelength of light. By this the receptor acquires waveguide properties. Further reduction in the receptor size is therefore impractical, since smaller receptors are less likely to be affected by photons as incident photons would more often be scattered or otherwise prevented from reaching inside the receptor to be absorbed by the photopigments (Synder and Miller, 1977).

The second limitation due to receptor size is the noise caused by the quantum nature of light. Even in steady light the photons ( $N$ ) arrive randomly, causing the light level to fluctuate. This fluctuation can be considered as noise ( $\alpha$ ) whose root mean square amplitude is the square root of the total amplitude of the light signal ( $\alpha$  rms noise =  $N^{1/2}$ ). As receptors get smaller, each one captures a smaller number of photons and the signal to noise ratio becomes smaller (as  $N$  decreases,  $N/N^{1/2}$  decreases). The following calculations illustrate this point. From psychophysics (Blackwell, 1946), we know that for a luminance difference to be detectable, the difference must be about 1% or greater. This implies that for high resolution situations (where the light signal falling on the neighboring receptors differs and the information contained in that variation must be preserved) there must be at least a 1% difference between receptors (to allow the detection of the difference). Therefore, in order to preserve the variation, the noise must be below 1%. (If the noise were greater than 1% of the average luminance, then noise would become confused with signal.) Now for the noise to be below 1%, a receptor must capture  $10^4$  photons per integration time, since  $\sqrt{10^4}$  is  $10^2$ , and  $10^2/10^4$  is 1%. If the receptor radius is  $4 \mu\text{m}$  and the integration time 20 msec (both numbers from the cat area centralis), the signal light level must be about  $5 \times 10^8$  photons/deg<sup>2</sup>·sec ( $225 \mu\text{m} = 1 \text{ deg}$ ). This means that the light level must be in the photopic range before receptor noise ceases to limit acuity. Smaller receptor sizes would necessitate even higher light levels.

#### Neural Stage

The neural processing of spatial information shows considerable convergence from receptors to ganglion cells. In the primate retina the

ratio of the number of all receptor cells to ganglion cells is about 100:1, while the ratio of cones to ganglion cells is about 8:1. In the area centralis of the cat retina these ratios are similar (Rodieck, 1973). After the ganglion cell level the number of cells expand again. The primary visual area of the cortex has about 100 times as many cells as there are ganglion cells. Therefore the ganglion cells seem to be a bottleneck for information channels. One possible reason for the low number of ganglion cells compared to the number of either receptors or cortical visual neurons is to save space. Since each ganglion cell gives rise to an axon which is very long (compared to most C.N.S. axons), each ganglion cell occupies many times the space needed by other visual neurons. An efficient method of organizing such a system would be to minimize the number of costly "long lines" (ganglion cells), even if that involved somewhat elaborate information processing before and after the ganglion cell level.

The key question introduced by the low ratio of ganglion cells to receptors is how the ganglion cell receptive fields are organized to minimize any loss of acuity due to this convergence.

In almost all of the electrophysiologic investigations of acuity at the ganglion cell level there has been an implicit or explicit (Hubel and Wiesel, 1960; Cleland *et al.*, 1968; Wässle *et al.*, 1973) assumption that the smaller the receptive fields are, the better acuity is. This idea has seldom been questioned because it seems so intuitively reasonable. In the next section, this idea will be analyzed, but first we should see the evidence for this idea. The experimental basis for associating high acuity with small receptive fields comes from work done by Enroth-Cugell and Robson (1966) on ganglion cells in the cat retina. They employed a technique similar to the Modulation Transfer Function measurements which characterized the optics. A modification of that technique was required for ganglion cell analysis since the output of the ganglion cells is not a linear function of the input. Instead, they presented one spatial sine wave grating frequency at a time and varied the grating's contrast until a particular ganglion cell response criterion was met (usually threshold). By using the same criterion for all frequencies, Enroth-Cugell and Robson found, in effect, the contrasts at the different frequencies which produced the same input to the ganglion cell. (Similar ganglion cell responses insure similar ganglion cell inputs since the input-output function in the ganglion cell is monotonic).

Once a set of measurements were made of the contrast for different frequencies to achieve the criterion, these numbers could be plotted as in Figure 3. This is a description of the responses in the frequency domain. If the system is linear, symmetric and homogeneous, the frequency measurements can be reverse Fourier transformed into the spatial domain. For one type of ganglion cell the cell's input is apparently a fairly linear function of the stimulus light (the X-cell class). The

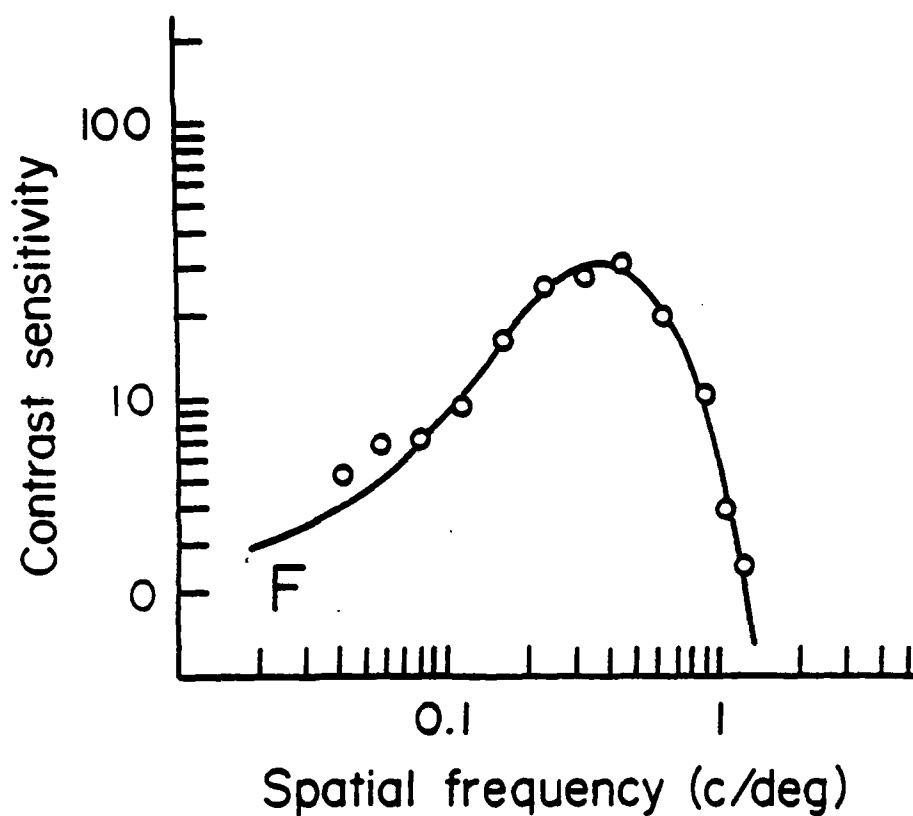


Figure 3: The contrast sensitivity function for a cat retinal ganglion cell. Contrast sensitivity is the inverse of the contrast ( $1/\text{contrast}$ ) and contrast is the maximum luminance minus the minimum luminance divided by the maximum luminance plus the minimum luminance ( $(L_{\text{max}} - L_{\text{min}}) / (L_{\text{max}} + L_{\text{min}})$ ). For each of a series of frequencies the minimal contrast necessary to achieve a threshold response is measured (From Enroth-Cugell and Robson, 1966).

requirements of homogeneity and symmetry can also be met, at least to a local approximation. This local homogeneity and symmetry are sufficient since the result of the frequency to spatial domain transform is local.

The transform into the spatial domain gives the spatial sensitivity function of the cell for the particular criterion used. The spatial sensitivity function can in turn be considered as the difference between two gaussian functions. Figure 4 illustrates these functions. Finally the two gaussian functions can be interpreted as a center region function and a surround region function. Enroth-Cugell and Robson interpreted their data in just this way and found that the cells with the best high spatial frequency sensitivity (the best acuity) had the smallest center region gaussian functions. This analysis fit nicely with the "common sense" idea that small fields would show greater acuity and has received very wide support (Harter, 1970; Sachs et al., 1971; Campbell et al., 1973; Maffei and Fiorentini, 1973).

#### A THEORETICAL APPROACH TO THE ROLE OF GANGLION CELL RECEPTIVE FIELDS IN ACUITY

This section is a theoretical approach to the question of receptive field size and its implication for acuity. An analysis of three topics will be presented. In the first part the Contrast Sensitivity Function of gaussian receptive field models, will be analyzed. In the second part, retinal ganglion cell receptive fields will be analyzed in terms of general properties of small and large field models, and in the third part, a computer simulation of small and large field models is given to show their relative sensitivity to noise.

##### Contrast Sensitivity Function

Measurements of the C.S.F., the reverse Fourier transform of those measurements and then separation of the result of that reverse transform into two gaussian functions seems to imply that good high frequency sensitivity comes from small receptive fields (Enroth-Cugell and Robson, 1966). The initial manipulation by reverse Fourier transformation can be fairly well justified but the interpretation in terms of receptive fields is weak.

The gaussian functions were chosen because they seem to be good models of the center and surround regions of some ganglion cells as measured with various spot stimuli (Wagner et al., 1960; Rodieck and Stone, 1965). However, other functions which would also fit the reverse transform can be equally well applied and these would indicate very different receptive field properties. For example, the C.S.F. from human psychophysical measurements is commonly interpreted as the difference between two exponential functions (Campbell and Green, 1965).

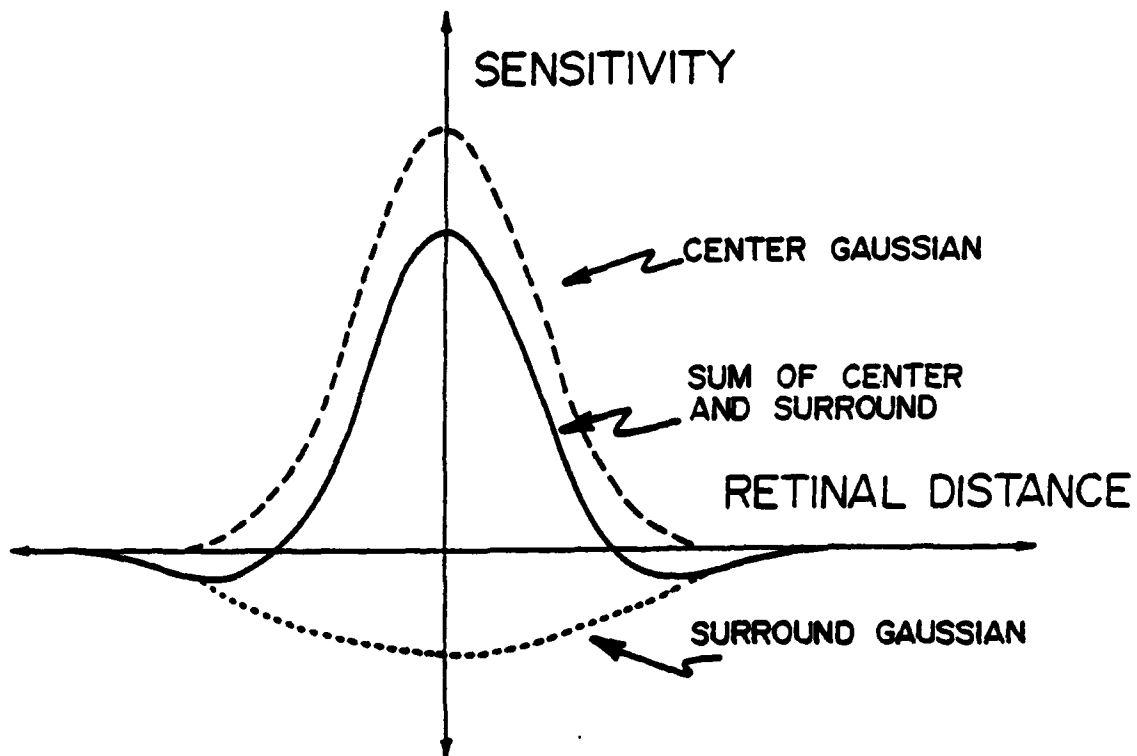


Figure 4: The reverse Fourier transform of the C.S.F. The solid line is the usual form of a reverse Fourier transform of the C.S.F. (Figure 3). According to the C.S.F. to gaussian fields model this may be interpreted as the difference between a gaussian curve representing the center (dashed line) and a gaussian curve representing the surround (dotted line).

There are two types of experimental data which cast serious doubt upon the nearly arbitrary use of gaussian functions to describe receptive field regions. The first type of data is the results of C.S.F. measured for an animal as a whole (behavioral measurements) compared to the results of C.S.F.s measured for single units. In the three animals which have received the bulk of experimental attention (monkey, cat and goldfish) the C.S.F.s show from 2 to 10 times the acuity predictable from single unit measurements (monkey, DeMonasterio and Gouras, 1975; cat, Wässle and Creutzfeldt, 1973; Bisti and Maffei, 1974; goldfish, Northmore and Dvorak, 1979). In other words the measured acuity implies (according to the C.S.F.-receptive field model) that there must be receptive field sizes much smaller than have ever been found. The standard explanation for this discrepancy is that these very small receptive field ganglion cells exist but have simply not yet been measured (Wässle and Creutzfeldt, 1973). This is of course possible, but in each of these animals many thousands of units have been sampled and the gap between the predicted smallest fields and measured smallest fields still remains significant.

The second type of experimental result which conflicts with the C.S.F.-receptive field model is the receptive field measurements made at varying luminance levels. The C.S.F. shifts smoothly to lower frequencies (lower acuity) as luminance is lowered (Le Grand, 1967; DeValois *et al.*, 1974). The C.S.F.-receptive field model predicts that since the C.S.F. is shifting smoothly as luminance is falling then the receptive fields must smoothly increase in size. This in fact does not happen. Field sizes do not change as luminance falls, except for a rather abrupt shift in size that occurs upon the change from cone to rod vision (Barlow, Fitzhugh and Kuffler, 1957; Enroth-Cugell and Shapley, 1973).

There is another criticism to be considered which applies to any model that requires the best acuity to reside in individual, small receptive field cells. These models fail to consider the possible increase in acuity from a combined contribution of many cells. This idea will be discussed further in the next section. Here, only its specific application to the C.S.F.-receptive field model will be considered.

If we accept, for the moment, the C.S.F.-receptive field model and its implication that a cell's C.S.F. directly predicts a particular receptive field size, it is still possible for an animal to achieve just as good high frequency resolution with large fields as with small ones. Large field ganglion cells will resolve as well as small field ganglion cells in the case where the high frequency fall off of the C.S.F. is linear, as it may be in the cat (Campbell *et al.*, 1973) and goldfish (Northmore and Dvorak, 1979).

The high frequency end of the C.S.F. can be characterized by the cutoff frequency,  $f_c$ , which is the highest frequency to which a response



is obtained with 100% contrast. In other words the spatial grating of frequency  $f_c$  provides only just enough signal to achieve some threshold signal-to-noise ratio (S/N). If the high frequency end of the C.S.F. is linear, doubling the frequency means the contrast must be doubled in order to maintain the same criterion response or signal-to-noise ratio. Therefore, if the contrast is held at what was a previous threshold value while the frequency is doubled, the signal will be one-half the necessary threshold value, as will the S/N. If the receptive fields are twice as large as the behavioral C.S.F. transform would predict then those cells will have a  $f_c$  at one half the value of the behavioral  $f_c$ . This can be shown rigorously as follows:

In the C.S.F. to Gaussian field model the gaussian functions are:

$$\text{Center region sensitivity: } k_c r_c^2 \exp [-(\pi r_c f)^2] \quad (1)$$

$$\text{Surround region sensitivity: } k_s r_s^2 \exp [-(\pi r_s f)^2] \quad (2)$$

where:  $r_c$   $\equiv$  center region radius  
 $r_s$   $\equiv$  surround region radius  
 $k_c$   $\equiv$  weighting constant for the center  
 $k_s$   $\equiv$  weighting constant for the surround

and defining  $S(f) \equiv$  cell sensitivity at frequency  $f$

$$S(f) = k_c r_c^2 \exp [-(\pi r_c f)^2] - k_s r_s^2 \exp [-(\pi r_s f)^2] \quad (3)$$

[from Enroth-Cugell and Robson, 1966]

Now, at the cutoff frequency,  $f_c$ ,  $S(f_c)$  is zero and,

$$k_c r_c^2 \exp [-(\pi r_c f_c)^2] - k_s r_s^2 \exp [-(\pi r_s f_c)^2] = 0 \quad (4)$$

$$\text{or, } \frac{k_c r_c^2}{k_s r_s^2} \exp [-(\pi r_c f_c)^2] = \exp [-(\pi r_s f_c)^2]. \quad (5)$$

If we define  $C$  as  $k_c r_c^2 / k_s r_s^2$ , then increasing the receptive field size by some factor  $n$  means  $C_{\text{new}}$  is the same as  $C_{\text{old}}$  since:

$$k_c (n r_c)^2 / k_s (n r_s)^2 = k_c r_c^2 / k_s r_s^2 \quad (6)$$

which reduces to  $C$ .

Thus, increasing receptive field size by  $n$ :

$$C \exp [-(\pi (n r_c) f_c)^2] = \exp [-(\pi (n r_s) f_c)^2] \quad (7)$$

$$C = \exp [-(\pi (n r_s) f_c)^2] / \exp [-(\pi (n r_c) f_c)^2] \quad (8)$$

$$C = \exp [-(\pi (n r_s) f_c)^2 + (\pi (n r_c) f_c)^2] \quad (9)$$

and taking the natural logarithm

$$\ln C = -(\pi (n r_s) f_c)^2 + (\pi (n r_c) f_c)^2 \quad (10)$$

$$\ln C = (r_c^2 - r_s^2) \pi^2 n^2 f_c^2 \quad (11)$$

$$\text{so, } f_c = (\ln C)^{\frac{1}{2}} \frac{1}{(r_c^2 - r_s^2)^{\frac{1}{2}}} \left( \frac{1}{\pi} \right) \left( \frac{1}{n} \right) \quad (12)$$

$$\text{and } f_c \propto \frac{1}{n} \quad (13)$$

thus, increasing the field size by a factor  $n$  decreases the cutoff frequency by  $n$ .

In addition, at the behavioral  $f_c$  the S/N of the large field cells will be one-half the necessary threshold value. However, since these fields have 4 times the area of the small fields there will be 4 times the overlap of fields. This overlap may be advantageous because averaging will improve the S/N for the large field cells in combination by the square root of the overlap factor ( $\sqrt{4}$ ) or 2 which would then bring the behavioral  $f_c$  to just threshold.

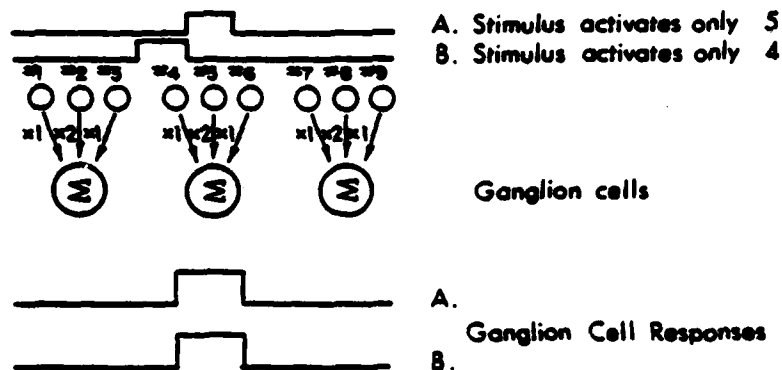
This combining procedure will work for any size fields. Any set of fields which are some factor  $A$  larger than the behavioral C.S.F. predicts, will give  $A^2$  more area and thus, more overlap, so the tendency to reduced acuity caused by the increased field size (factor of  $A$  reduced spatial frequency sensitivity) will be balanced by a better S/N (S/N will improve by the square root of the overlap,  $\sqrt{A^2}$  or  $A$ ). In any case in which the C.S.F. has a linear high frequency end, and averaging is employed, the acuity is independent of field size.

#### Large Field Models

Every region of every retina has more receptors than ganglion cells (although, if all types of ganglion cells are included the primate fovea numbers are close). The problem to be resolved in the organization of the ganglion cells receptive fields is the preservation of the spatial resolution of the receptors while compressing the information into the reduced number of ganglion cells.

Since the number of ganglion cells is not as large as the number of receptors, a point-to-point representation of the image cannot be preserved in every stage of the visual system. Indeed, merely to connect sufficient receptors to each ganglion cell to satisfy the ratio of receptors to ganglion cells would not only not solve the visual acuity problem, but make it much worse. The blocks of receptors that would result, each block converging on one ganglion cell, would produce a point-to-point representation system but one which would be equivalent to a model with larger receptors. Larger receptors would produce a coarser retinal grain which would obviously degrade visual acuity. However, paradoxically, even larger receptive fields will be better; that is larger receptive fields with overlap. Figure 5 illustrates how larger fields with overlap produce better spatial resolution than small fields. In this type of model, each receptor will have connections to several ganglion cells. Such a hook-up gives the possibility of pre-

## SMALL GANGLION CELL RECEPTIVE FIELDS



## LARGE GANGLION CELL RECEPTIVE FIELDS

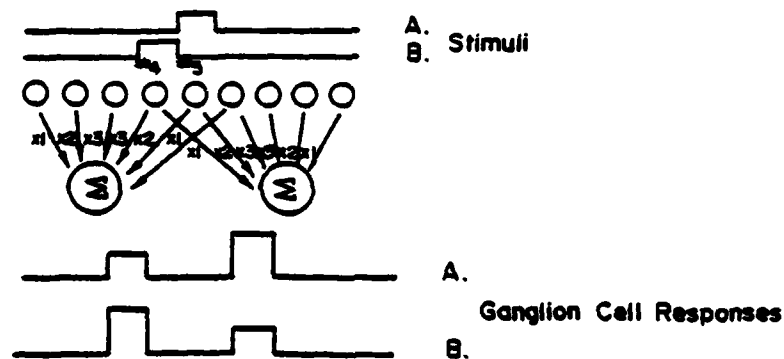


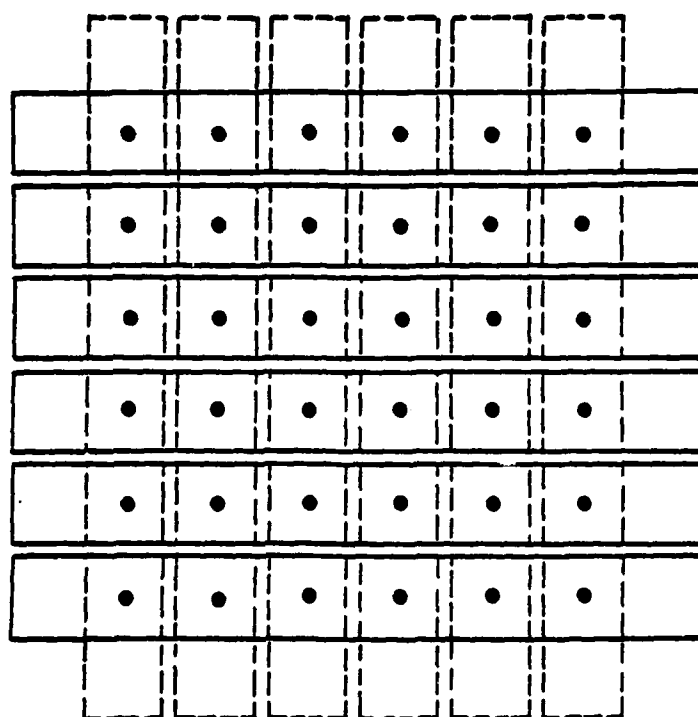
Figure 5: A simple model suggesting that large ganglion cell receptive fields preserve information about stimulus location which is lost by small fields. In this model the ganglion cell response is the sum of the weighted receptor responses. For the small fields the central receptor's response is multiplied by a factor of 2 while the two flanking receptor's responses are multiplied by a factor of 1. The connections in the small field model produce the smallest fields possible if there are 3 times as many receptors as ganglion cells. With this hook-up, detail available at the receptor level is lost at the ganglion cell level. For example, as is shown in the illustration the ganglion cell level cannot distinguish between 2 units of response in receptor #4 and 1 unit of response in receptor #5.

The large ganglion cell receptive field receives input from 6 receptors, weighted by factors of 1, 2, 3, 3, 2, 1. The connection for the large field are also appropriate for a 3 to 1 ratio of receptors to ganglion cells. However, in this case the ganglion cell level responses caused by adjacent receptors are not simple multiples of one another, so responses in receptors #4 and #5 (illustrated) are distinguishable.

serving the spatial information available from each receptor. However, in order to preserve the receptor information, each receptor must have a unique representation (or input) to the ganglion cells. The reason for this is that if two receptors have the same representation then, obviously, their responses will be indistinguishable, so resolution between the two receptors will have been lost. A simplified schematic of a system which could accomplish unique representation with a low ratio of ganglion cells to receptors is shown in Figure 6. The receptors are arranged in a square array while the ganglion cell receptive fields are oblong and form vertical and horizontal slits. The combined signals from the ganglion cells designates a unique location by a sort of Cartesian grid. However, receptive fields with these oblong spatial characteristics are not actually seen in ganglion cells so a further stage of refinement is necessary.

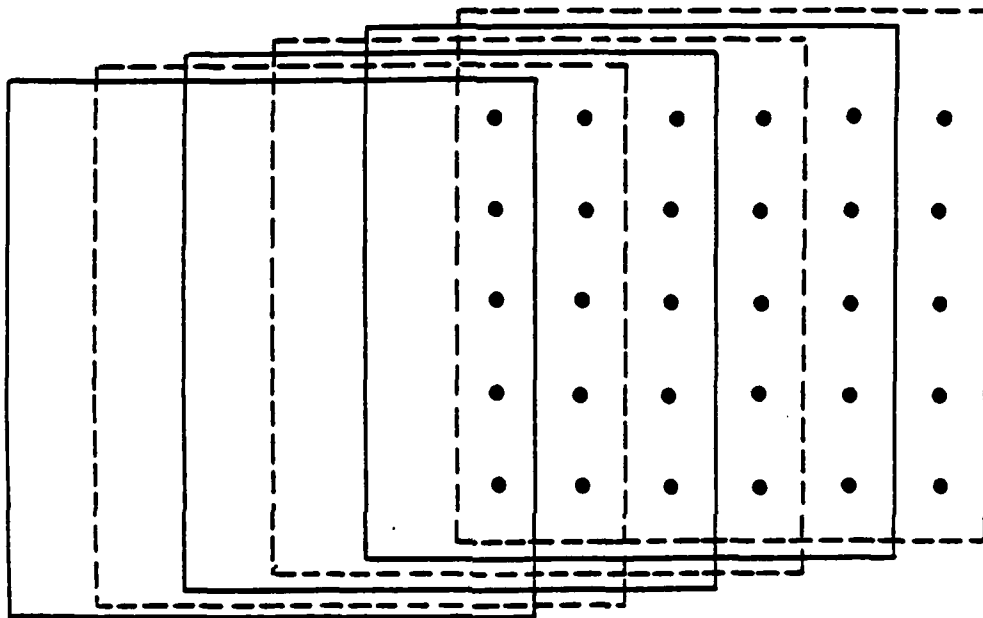
The physiological data on ganglion cell receptive fields is most consistent with a round or elliptical shape. This round or elliptical shape can be approximated by the square fields shown in Figure 7. This model operates in a more complicated but analogous fashion to the oblong slits shown in Figure 6 to locate uniquely all of the points on the surface of the retina. For regular receptive field shapes (such as circles, ellipses and squares) a receptor's representation in the ganglion cell array is unique among all receptors if its total representation is different from its four neighbors. To establish this difference some border of a receptive field must pass between each receptor and its neighbors. This in turn requires that all borders summed together must be twice the length (in number of receptors) as the number of receptors in the retina. (A receptor requires one-half of a receptor length border between it and each of its 4 neighbors. The other one-half of the border is provided by the neighbor.) The number of ganglion cells needed to provide that much border obviously depends on the size of each receptive field. For a minimal unique receptor representation the larger the receptive field the fewer the necessary number. If there are  $10^3$  receptors in a  $10^3$  by  $10^3$  array and the ganglion cell receptive fields are 10 by 10 receptors, then  $5 \times 10^4$  ganglion cells are needed. The ganglion cell to receptor ratio is 1:20. This number changes slowly as the ganglion cell receptive field gets larger or smaller. The upper limit on the size of the field is reached when each ganglion cell is connected to one-half of the receptors. (Including more than half of the receptors would reduce the border length. This can be best illustrated by thinking of the border as excluding certain receptors. That border will shrink as the number of receptors to be excluded is reduced below half of all the receptors.)

An organization of receptive fields that places a great emphasis on the inclusion or exclusion of a receptor from the receptive field would need to have very sharply defined borders. It is interesting to speculate that the production of just such borders is one of the functions of the center-surround organization of the ganglion cell receptive fields. The sensitivity profiles of these borders are examined in the experimental section.



**OBLONG GANGLION CELL RECEPTION FIELDS**

Figure 6: Localization of retinal stimulus by ganglion cell receptive fields. The oblong receptive fields have horizontal and vertical (row and column) overlap in such a way as to allow unique identification of each retinal receptor. This arrangement is analogous to a Cartesian coordinate system (From Wolbarsht and Ringo, 1978).



GANGLION CELL RECEPTIVE FIELD BORDERS.

Figure 7: Localization of single points on the retina by interaction of ganglion cell receptive fields. The square fields shown here overlap in such a way that unique localization is possible. There are additional sets of ganglion cells (not shown) which are displaced in the vertical direction in successive rows. This gives the same localization in the vertical plane as is illustrated in the horizontal plane. The number of ganglion cell receptive fields of this type needed to give unique localization in relation to a given number of receptors is discussed in the text. The square ganglion cell receptive fields are equivalent to the circular fields in the real retina. The same analysis applies when the ganglion cell receptive fields have comparable displacement within the receptor matrix (From Wolbarsht and Ringo, 1978).

The theoretical minimum for the number of ganglion cells required to uniquely represent  $10^6$  receptors is just 20. This is achieved with admittedly unrealistic receptor to ganglion cell connections such that each ganglion cell receives input from one-half of the receptors and the ganglion cell receptive fields are independent of one another. That is, if a receptor is connected to some particular ganglion cell, the a priori chance of its being connected to some other particular ganglion cell is still one-half. Each receptor's connections to the ganglion cells can then be thought of as a binary number, 1 if connected and 0 if not connected. The ganglion cells would be represented by their place in this number.  $2^{20}$  is 1,048,576 so that, theoretically, 20 ganglion cells could uniquely represent each one of  $10^6$  receptors.

In the mid-range, larger ganglion cell receptive fields produce more sensitivity for the detection of single points. This performance can be improved by introducing other parameters of the receptors based on the physiologic data known at present. One requirement would be to consider varying sensitivities within a receptive field. If the pattern of each receptive field sensitivity is different, then the possibility that a few ganglion cells can identify the visual stimulus is very good. As an example, if three ganglion cells have receptive fields covering exactly the same set of receptors and each of the three ganglion cells has a different sensitivity profile (such that there is no mutual linear dependence) good localization is possible. One particular set of sensitivity profiles that will work very well is to have one ganglion cell with a flat sensitivity profile, a second linearly decreasing from the center, and the third exponentially decreasing from the center. These three cells can simultaneously determine the position of the light and whether it is one spot or two. The flat sensitivity profile cell will describe the total quantity of light. This taken in combination with the linearly decreasing profile cell defines the exact radius at which a point of light would be located. A further comparison with the exponentially decreasing sensitivity profile will determine whether the previously defined radius is proper for a single stimulus point or whether the light distribution would be better represented by several sources. An estimate of the maximum size of such receptive fields can be made if it is assumed that a just noticeable difference between receptors along a radius will result if each receptor is 2% less sensitive than its inside neighbor (the 2% figure is about the j.n.d. for cat retinal ganglion cells). For the linear receptive field the radius would be limited to 50 receptors, and for a 2 log unit exponentially decreasing receptive field profile cell the radius would be limited to 232 receptors.

#### Computer Simulation

Large and small receptive field ganglion cells were modeled in a computer simulation to assess their relative sensitivity to noise. Noise is an inherent part of any visual task. There are two sources of

noise considered for this model: first, the quantum fluctuation noise present in the arrival of photons from any source; second, the inherent noise within the receptors. The quantum noise is very important at low light levels and becomes progressively less so as the light level is increased. (At luminance level  $L$  the noise average amplitude is  $\sqrt{L}$  so the signal to noise ratio increases as  $L$  increases.) The inherent receptor noise is seen in intracellular recordings from photoreceptors, and it may be due to spontaneous thermal breakdown of photopigment (Baylor and Fourtes, 1970; Burke and Hayhow, 1968; Barlow and Levick, 1969). As far as they affect the ganglion cell, these sources of noise are equivalent so they have been modeled as one noise component. Only the noise due to receptors was studied since, in this study, any noise due to ganglion cells will obscure ganglion cell signals equally regardless of the cell's receptive field size.

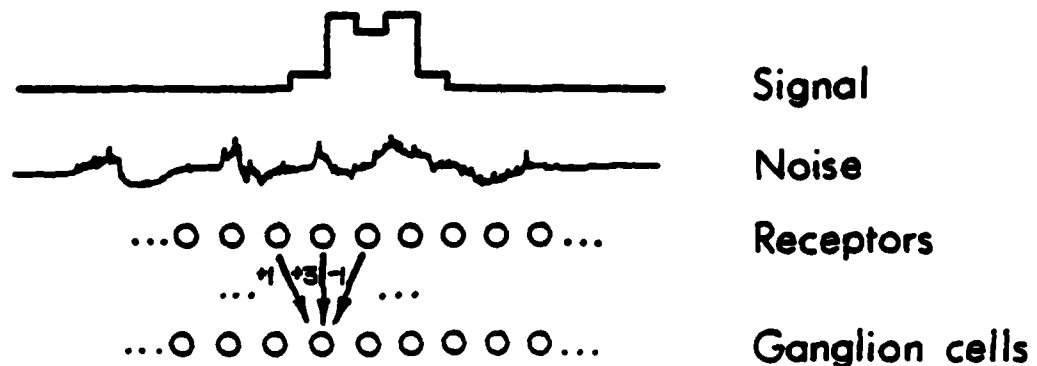
The basic features of the model are illustrated in Figure 8. An array of elements (receptors) are "stimulated" by a standard acuity test. This test is to distinguish between two points of light, which have been modeled as smeared across a few receptor elements as a real point source of light would be optically smeared across receptor cells. The receptors receive an additional input of noise. The noise is modeled by choosing a value randomly from a normal probability distribution for each receptor element. The normal distribution centers on zero with a standard deviation of 25% of the highest value of the "signal light". Noise values were constrained to be less than 50% of the highest signal light value at all times.

Two types of receptive fields were modeled. One was a small field and received input from only 3 receptors, a central receptor multiplied by a factor of +3 (the "center") and two flanking receptors multiplied by a factor of -1 (the "surround"). The other receptive field was a large type and received input from 13 receptors. These receptors were multiplied respectively by -1, -3, -5, -2, 2, 6, 9, 6, 2, -2, -5, -3, -1 (The positive multiplicative constants are the "center" and the negative multiplicative constants are the "surround"). The particular constants were chosen to match the experimentally measured receptive field profiles (See following experimental results section.).

The two field types were compared for immunity to noise by running each field with just the signal (the modeled two points of light) and comparing these runs to runs made with noise added. The results were normalized before comparisons were made. Table 1 shows the results with the small field model for one computer run with just the signal (third column) and one run with the signal plus noise (fifth column). The righthand column of Table 1 shows the difference caused by the noise. The average difference, as a per cent of the maximum value of the signal alone run (18) is 17.5%. This per cent figure was found for 10 different runs. The grand average of "ganglion cell" response fluctuation was 37.7%. Table 2 shows results with the large field model. For this run the average "ganglion cell" response fluctuation was 3.9%. In 10 different runs, the



## Model for Computer Simulation



Receptor no.  $i$  response =  $R(i)$  = Signal (at  $i$ ) + Noise (at  $i$ )

Ganglion cell no.  $i$  response =  $-1(R(i-1)) + 3(R(i)) - 1(R(i+1))$

Figure 8: The basic features of the ganglion cells model used in the computer simulation. The signal is two points of light modelled as smeared across 5 receptors, having values in arbitrary units of 4, 10, 8, 10, 4. The receptor elements also receive noise input. The value of the noise is selected randomly from a normal distribution centering on zero with a standard deviation of 2.5 units (same arbitrary units as the signal). The noise input to a receptor was not allowed to exceed 5 units. The ganglion cell responses are the weighted sums of the receptor responses (signal plus noise).

Two forms of weighted sums were used. One (shown in the figure) modelled a small ganglion cell receptive field;  $G(i) = -1(R(i-1)) + 3R(i) - 1(R(i+1))$  where  $G(i)$  is the response of the  $i$ th ganglion cell and  $R(i)$  is the response of the  $i$ th receptor. The other form modelled a large ganglion cell receptive field;  $G(i) = -1(R(i-6)) - 3(R(i-5)) - 5(R(i-4)) - 2(R(i-3)) + 2(R(i-2)) + 6(R(i-1)) + 9(R(i)) + 6(R(i+1)) + 2(R(i+2)) - 2(R(i+3)) - 5(R(i+4)) - 3(R(i+5)) - 1(R(i+6))$ .

Table 1  
Small Field Model

Place no.	Signal	G(i) for Signal	Noise for Run #1	G(i) for Signal Plus Noise	Difference   G(i) [Signal] - G(i) [Signal + Noise]
1		0			
2		0			
3		-4	0	-3	1
4	4	2	-1	-1	3
5	10	18	0	19	1
6	8	4	0	2	2
7	10	18	2	23	5
8	4	2	1	5	3
9		-4	-2	-11	7
10		0			
11		0			

$\overline{22} =$  Total error

3.1 = Average error

17.5% = Average error as  
per cent of  
maximum value

Compilation of one computer run for the small ganglion cell receptive field model. The average error introduced by the noise was 17.5%. G(i) is the  $i^{\text{th}}$  ganglion cell's response.

Table 2

## Large Field model

Place no.	Signal	G(1) for Signal	Noise for Run #1	G(1) for Signal Plus Noise	Difference   G(1) [Signal] - G(1) [Signal + Noise]
1		0	0		
2		0	0		
3		0	0		
4		0	-2		
5		0	1		
6		-4	0		
7		-22	-1	-28	6
8		-58	-2	-59	1
9		-92	2	-93	1
10		-86	-1	-95	9
11		-34	0	-45	11
12	4	72	-1	60	12
13	10	174	0	170	4
14	8	208	0	210	2
15	10	174	2	187	13
16	4	72	1	85	13
17		-34	-2	24	10
18		-86	3	-46	40
19		-92	0	-52	40
20		-58	0	-38	20
21		-22	4	-21	<u>1</u>
22		-4	-4		183 = Total error
23		0	-5		12.2 = Average error
24		0	1		
25		0	0		<u>5.9%</u> Average error as
26		0	0		per cent of maximum
27		0	0		value

grand average "ganglion cell" response fluctuation was 12.5%. Thus, noise input to the small field model resulted in slightly more than three times the response fluctuation that resulted from noise input to the large field model.

#### EXPERIMENTAL APPROACH WITH NEUROPHYSIOLOGICAL TECHNIQUES TO THE SIZE OF GANGLION CELL RECEPTIVE FIELDS IN RELATION TO VISUAL ACUITY

##### Methods

The responses of single ganglion cells from the retinas of adult cats were recorded. The methods used in this study were generally the same as those described in a previous work (Wolbarsht and Ringo, 1979).

##### Foreword

The animals involved in this study were procured, maintained, and used in the accordance with the Animal Welfare Act of 1970, and the "Guide for the Care and Use of Laboratory Animals" prepared by the Institute of Laboratory Animal Resources-National Research Council.

##### Anesthesia and Surgery

All experiments were carried out on healthy adult cats under general inhalation anesthesia as described. Animals were initially anesthetized with ether. When a suitable depth of anesthesia was obtained, an intravenous infusion of gallamine triethiodide (Flaxedil) was initiated. The animal was then intubated and respired artificially with a ventilator (Harvard Apparatus Company Model 661). Anesthesia was maintained with 70% nitrous oxide/30% oxygen mixture in all animals throughout the experiment. Expired  $pCO_2$  was monitored continuously by a Beckman Model LB-1 medical gas analyzer with the aid of an indicator alarm (Electrodyne MS-25). In addition to the control of gas mixture flow furnished by the anesthesia machine (Ohio Chemical and Surgical Instrument Company, Model 212B), a manometer was installed to avoid any damage to the animal's lung from over-pressure during the inspiration and exhalation parts of the respiratory cycle.

The infusion of Flaxedil with dextrose and saline was continued throughout the experiment to assist in fixing the eyes. A local anesthetic (5% Lidocain ointment) was applied to the surface of the conjunctiva before an incision was made to insert the electrode into the eye, and to all other incision margins and pressure points. Animals were maintained at normal body temperature by means of a heating pad. These life support systems were adequate to maintain a cat in satisfactory physiological condition for 24 to 48 hours. The animals were sacrificed at the end of the experiment.

Although nitrous oxide, even at high pressures, does not produce surgical anesthesia (Brown et al., 1927; Venes et al., 1971), it has

been established that 60% nitrous oxide in oxygen produces a high degree of sedation and analgesia in the cat and monkey and is an adequate anesthetic where only mildly noxious stimulants are present; for example, the direct electrical stimulation of peripheral nerves at frequencies up to 3 Hz or foot pad shock (Venes et al., 1971). In our experiments, the animals are under deep ether anesthesia during all surgical procedures. The level of ether anesthesia was sufficient to terminate spontaneous respiration and the animals required artificial ventilation. In addition, all cuts were infiltrated with a local anesthetic. Only after surgery was ended was the ether discontinued and 70% nitrous oxide/30% oxygen used. The insertion of the electrode through the pars plana involved no pain and is similar to operations that are often carried on in humans with only a local anesthetic. The heart rate was continuously monitored and at no time were heart rate changes detected which could be associated with pain perception.

The galamine triethiodide (Flaxedil) drip is not required to relax the animal. It assists in establishing the high degree of eye immobility required for single cell retinal recordings (Enroth-Cugell and Robson, 1966). It has also been established that Flaxedil has no effect on retinal ganglion cell responses (Enroth-Cugell and Pinto, 1970). Because of these considerations nitrous oxide and Flaxedil have been routinely used by all workers in this field.

Nitrous oxide is used by us and others because it has been shown to have only slight effects on evoked CNS responses as compared to the strong central depression produced by other volatile anesthetics and barbiturates (Van Norren and Padmos, 1977). A depressive action in the retina has been seen with some of these anesthetics as well (Van Norren and Padmos, 1977). It is obviously important to minimize drug effects on the CNS when studying the activity of the visual system.

#### Optical Stimulus

The optical stimulator has been described previously (Wolbarsht, 1978) and has two channels with essentially equivalent pathways. Each channel could be varied independently and included a collimated region to allow the use of interference filters.

A Maxwellian view was used for the stimulus, and the field aperture of the optical stimulator was focused on the retina. The stimulus beam was approximately normal to the retina to eliminate any changes in the stimulus-response relations from the Stiles-Crawford effect. A third channel is available, which is suitable for chromatic adaptation of the entire retina through the series of Wratten filters.

However, for the present series of experiments, three changes were made in order to make spatial measurements as accurately as possible. First, the exploratory spot used to map the receptive fields had a

diameter of 3.5 minutes of arc. Second, a Wratten #21 filter was used in the stimulus beam to convert the white light to orange light (Wratten #21 blocks light of 520 nm and shorter wavelengths). Third, a two dimensional micromanipulator was used to accurately position the exploratory spot in the object plane of the stimulus beam. The smallness of the spot allowed for the measurement of localized sensitivities within the receptive field. The chromatic restriction of the stimulus beam further localized the spot image by reducing chromatic aberration. The micromanipulator insured accurate and repeatable positioning of the stimulus spot.

### Experimental Design

Most data points were measured with a constant response technique. That is, when any selected parameter of the stimulus was changed the intensity was varied sufficiently to obtain a response equal to the criterion one at the original test conditions. Some data points were obtained by a silent substitution technique in which the stimulus was alternated from a new wavelength to the original one, or from one spatial distribution to another while the intensity of the altered position was changed to minimize or eliminate the response. Although this technique has problems, as some ON responses may be confused with OFF responses, a selection of the proper type of chromatic adaptation usually allows a balance to be reached, and in this way quite accurate data can be obtained. Spatial isolation of the stimulus can also be used to assist in elucidating the spectral sensitivity within a ganglion cell receptive field as composed of the various cone systems in addition to the rod contribution.

### Results

The experimental results may be divided into two groups: those which describe the receptive field sizes and those which show some of the detail properties of the receptive field sensitivity profile.

Receptive Field Size: Receptive field center sizes were measured for 46 cells. Table 3 lists the center sizes of 19 X-cells, the class most likely to be responsible for high acuity vision (Cleland, Dubin and Levick, 1971; Stone and Fukuda, 1974), measured in the area centralis, the area of highest ganglion cell density in the cats retina. The average diameter of these units was 0.43 deg. The average diameter of the 3 W- (average diameter, 1.7 deg.) and 24 Y-cells (average diameter, 0.92 deg.) was much larger.

Receptive Field Sensitivity Profile: There are two widely used methods for examining receptive field sensitivities, the small exploratory spot method and the Ricco field plot method (Rodieck, 1973). The small exploratory spot method makes use of a small, intense spot of light to sample the sensitivity of a cell's receptive field. The Ricco plot method is the measurement of threshold intensity for a series of varying

Table 3  
Receptive Field Center Diameters

X-cells in area centralis (in degrees).

1) .4	9) .4	17) .35
2) .25	10) .35	18) .42
3) .6	11) .35	19) .35
4) .8	12) .35	
5) .4	13) 1.0	
6) .2	14) .5	
7) .4	15) .4	
8) .3	16) .35	

19 cells

Avg. = 0.43 degrees

Y-cells in area centralis

24 cells

Avg. = 0.92 degrees

W-cells in area centralis

3 cells

Avg. = 1.70 degrees

diameter circular stimuli centered on the cell's receptive field. This series generally runs from the smallest stimulus available to a stimulus much larger than the receptive field. The intensity of the stimulus which just reaches the cell's threshold is plotted against the stimulus size for the series of stimulus sizes. Both methods have been used as described previously (Wolbarsht and Ringo, 1979). Figures 9 and 10 are reproduced from this report to illustrate the sensitivity profile and a Ricco field plot for the receptive field of a ganglion cell located in the area centralis. The cell is an ON-center, OFF-surround, X-type. When measured with the small spot stimulus, the central ON response has a rounded or dome shaped sensitivity profile. Inhibition from the surrounding area makes an impression on the sensitivity profile only as the stimulus moves outside of the central area. On the other hand, the Ricco plot indicates by its  $45^\circ$  slope the almost complete summation of the stimulus to approximately  $115 \mu\text{m}$  ( $0.5^\circ$  degrees), but then sensitivity falls off as the stimulus increases its size. Presumably, this fall off occurs as the stimulus area grows larger because the peripheral inhibition begins to make a sizeable contribution to the response. Many other cells have been found with similar response functions, but there is a group which differs significantly.

This group of cells have a completely flat or a mesa shaped sensitivity profile for the center response. One example is shown in Figure 11. The Ricco field plot for this cell (Figure 12), surprisingly, showed very much the same type of response as shown in Figure 10, even though the sensitivity profiles of the central field in these cells (Figures 9 and 11) are much different for the small spot stimuli.

An examination of the slopes of the Ricco field plots of cells in and around the area centralis, as well as those for more peripheral cells, shows a remarkable similarity in shape between them. The variation between Ricco field plots in different parts of the cat retina seems to be quantitative rather than qualitative. This is true even when the area centralis is compared with the peripheral regions. Although the cells illustrated here are typical of the data, only a small number of cells are known in this much detail. For example, for many cells only the small spot sensitivity was completely measured while on others only the Ricco field plot was determined. This information was not sufficient to determine the proper model so the experimental protocol was revised to indicate data on displacement sensitivity.

Displacement Sensitivity: For these experiments the stimulus was a small spot of light (10 minutes of arc on the retina) rapidly switched between 2 positions, 10 minutes of arc apart. This stimulus was designed to measure the ganglion cell's receptive field sensitivity to displacement and was compared to the simple single spot flash sensitivity of the same unit. Figure 13 shows the two different types of sensitivity profiles measured on a unit in the area centralis, both profiles are of the predominant 556-nm cone system. The single spot



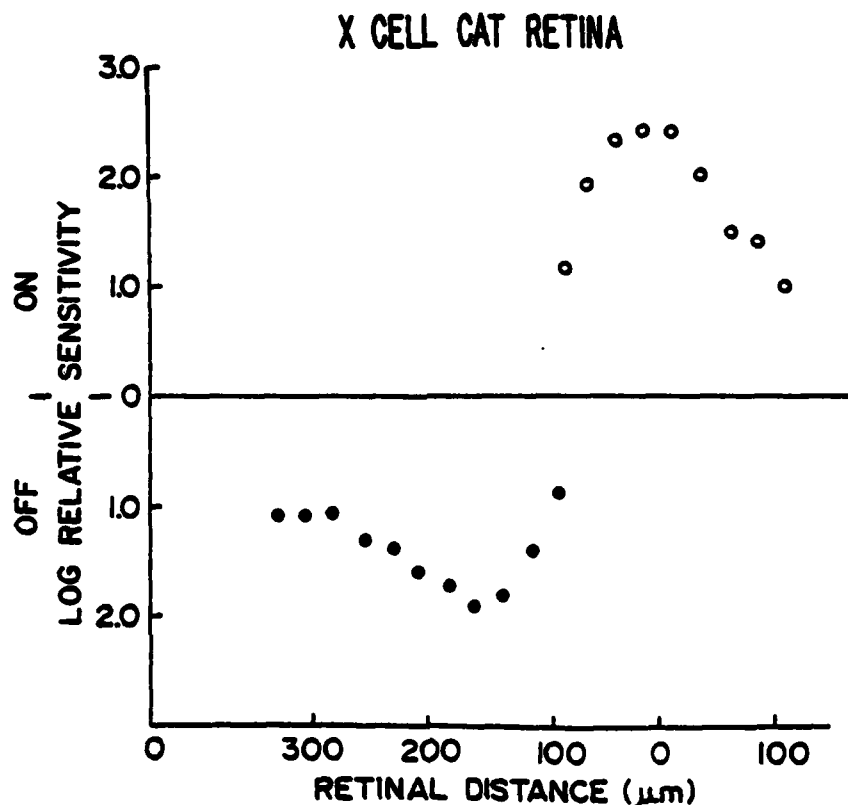


Figure 9: Sensitivity profile of an X type ganglion cell. The data points indicate the intensity required to give a criterion response. The ON response (open circles) in the center has a dome-shaped sensitivity profile. The stimulus is  $16 \mu\text{m}$  on the retina, or approximately  $0.07$  degrees of arc in the visual field similar to the point spread size. The sensitivity profile of the peripheral OFF response (filled circles) should be compared with the central ON response loss of sensitivity with distance. The OFF responses to the other side of the center are not shown. More information on the central ON response is given in the Ricco field plot in Figure 10, which suggests that the top of the sensitivity profile should be flatter (Reproduced from Wolbarsht and Ringo, 1979).

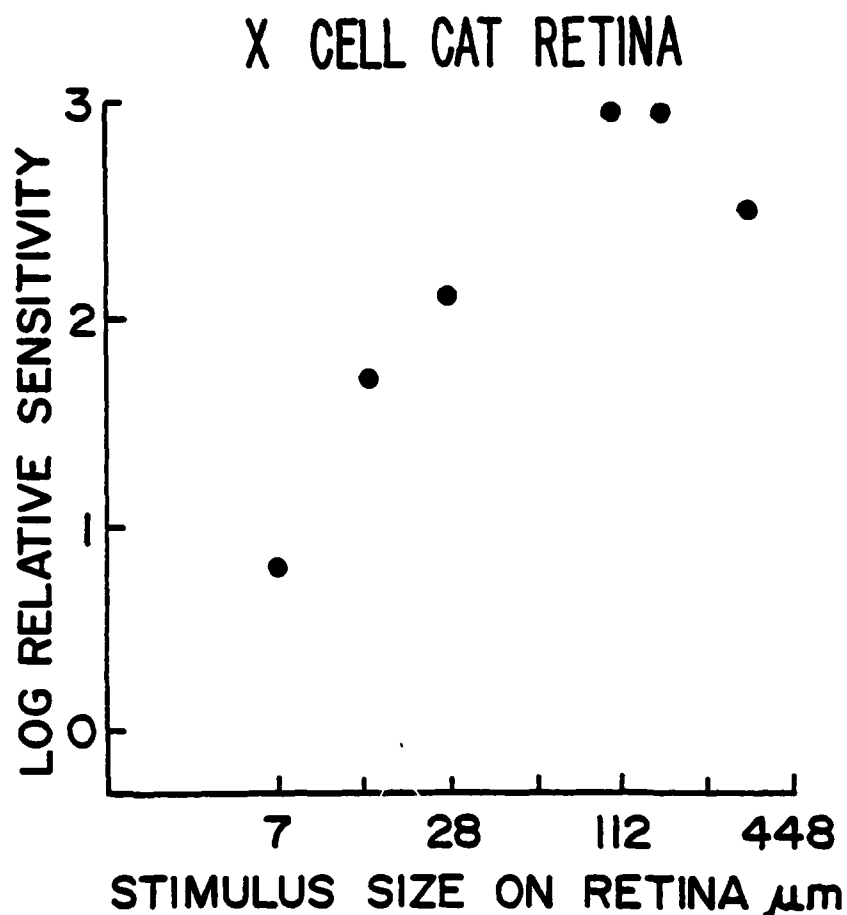


Figure 10: The Ricco field plot (area  $\times$  log intensity). The data points indicate the intensity required to give a criterion response for the ON response of a cat retinal ganglion cell (X type). The sensitivity profile of the central ON and peripheral OFF responses of this cell are shown in Figure 9. This Ricco field plot shows complete integration within the central ON response for approximately 110  $\mu\text{m}$ . The fall of sensitivity with increased stimulus area is probably due to the recruitment of inhibition from the antagonistic surround.

## CAT RETINA Y CELL

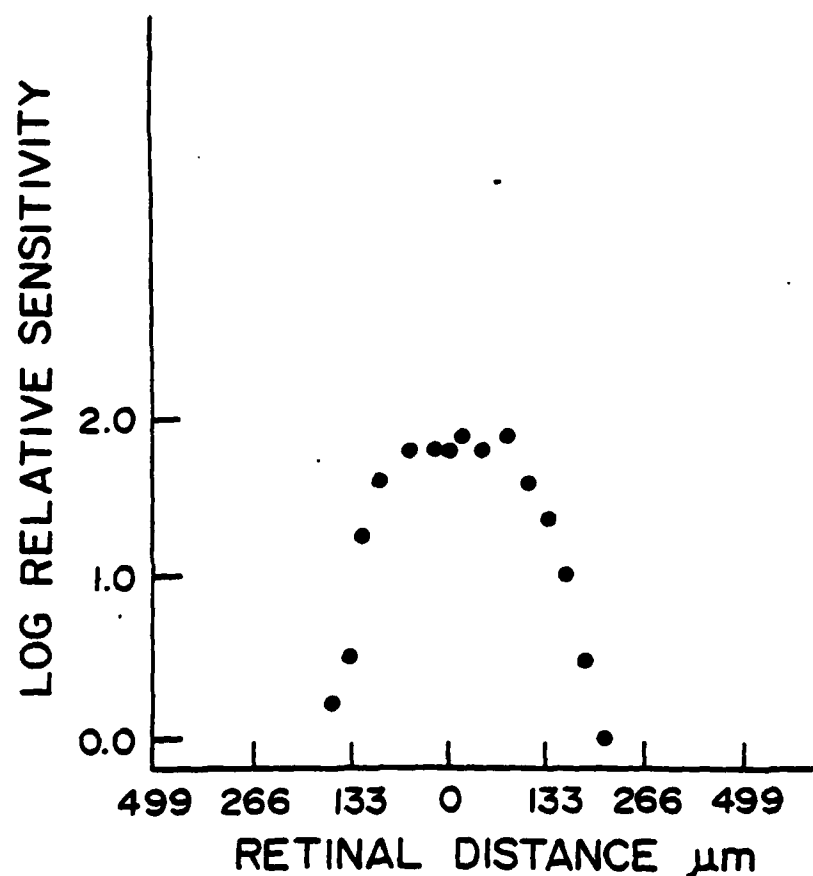


Figure 11: Sensitivity profile for central OFF response of a Y cell. The data points indicate the intensity required to give a criterion response. The flat top of the central response here should be compared to the profile of the cell shown in Figure 9. Although the central responses of those cells have quite different sensitivity profiles, their Ricco field plots are almost identical, as shown in Figures 12 and 10.

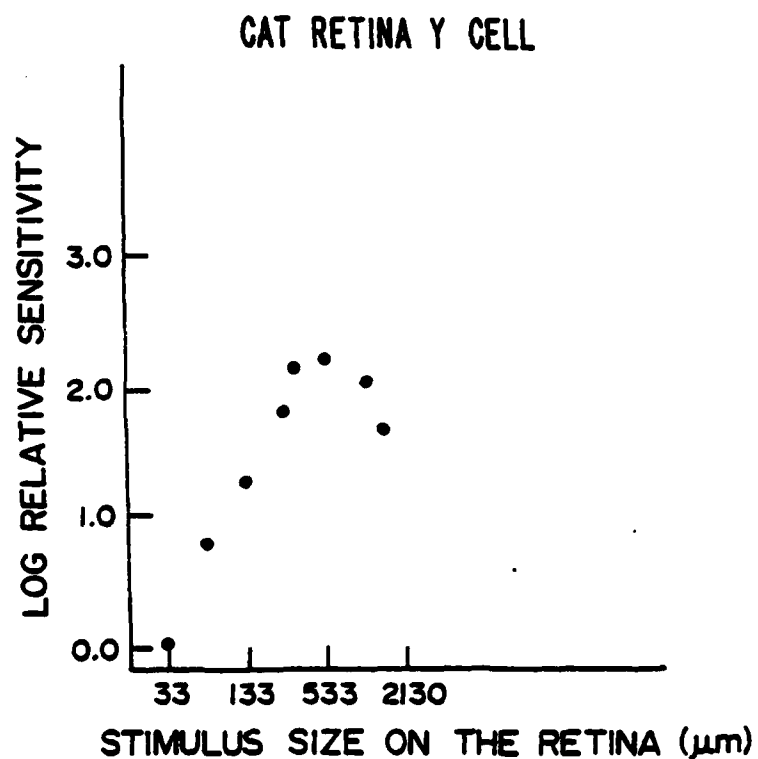


Figure 12: Ricco field plot (area  $\times$  log intensity). The data points indicate the intensity required to give a criterion type response for the OFF response of a Y cell in the cat retina. The sensitivity profile for the central OFF response of this cell is shown in Figure 11. Complete integration is shown up to about 400  $\mu\text{m}$ , which is larger than the flat part of the sensitivity profile for this cell.

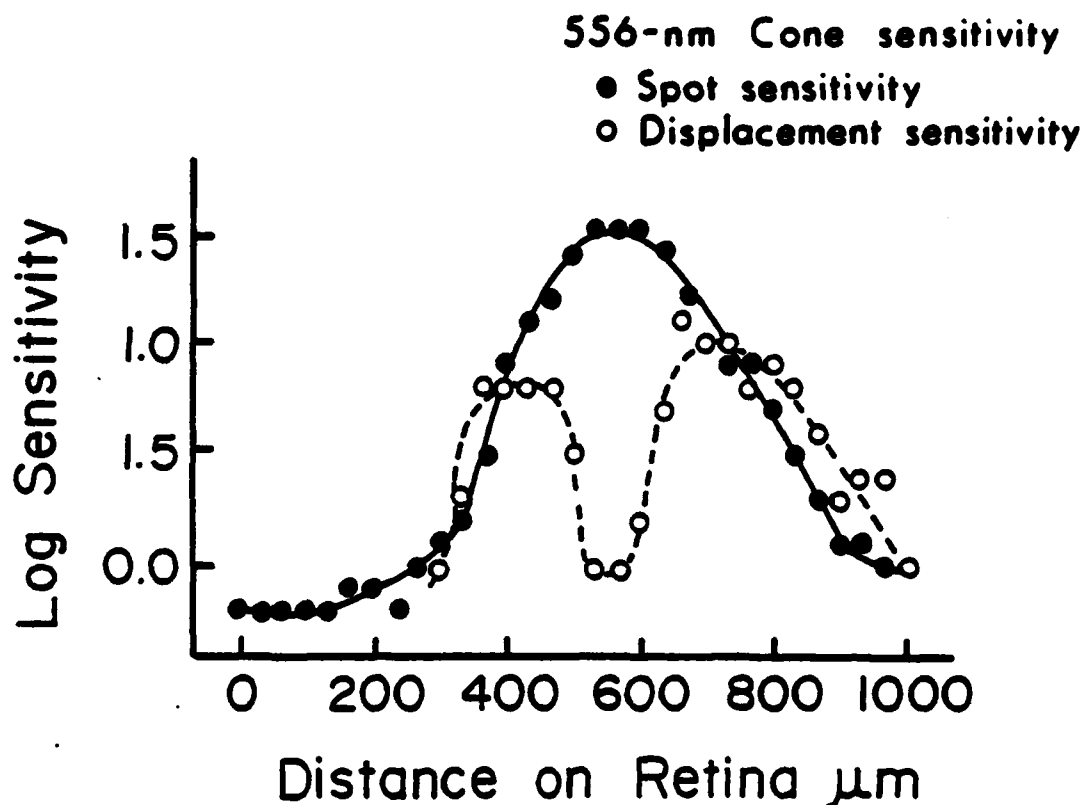


Figure 13: Displacement sensitivity of a ganglion cell. The spot sensitivity (filled circles) was measured with a  $35 \mu$  (10 minutes of arc) spot of yellow (580 nm) light. This spot was positioned then flashed at 0.5 hz until a threshold was determined for that position. The static spot sensitivity was measured every  $35 \mu$ . The blue background adapting light was provided by Wratten #47, equivalent for the rods to  $6.0 \times 10^{10}$  photons  $\text{deg}^{-2} \text{sec}^{-1}$  of 500 nm light. The blue background assured that the cell responses were mediated by the 556-nm cone.

The displacement sensitivity (open circles) was measured with a  $35 \mu$  (on the retina) spot jerk quickly (less than 0.1 sec) between two positions  $35 \mu$  apart. Between each displacement the cell remained unstimulated for 1 second. Each displacement sensitivity is plotted halfway between the two end positions. The displacement sensitivity was measured every  $35 \mu$  across the receptive field. The continuous and dashed curves were drawn in by the eye. Zero log units on the sensitivity axis is  $1.75 \times 10^{11}$  photons  $\text{deg}^{-2} \text{sec}^{-1}$  at the cornea, except that negative log sensitivity numbers are for the OFF response from the surround, and should be read as absolute values.

sensitivity for this cell has a very standard dome-like profile. The displacement sensitivity profile shows peaks at the center-surround border, not where the single spot sensitivity is highest but rather where the single spot sensitivity changes the most.

Figure 14 and 15 illustrates another unit in which the single spot and displacement sensitivity profiles were measured. Because this unit had a 450-nm cone contribution, two displacement profiles were measured, one for the 450-nm cone and one for the 556-nm cone. The displacement sensitivity profiles of the 556-nm cone (Figure 14) is similar to that shown in Figure 13 and has peaks at the center-surround border. However, the displacement sensitivity profile of the 450-nm cone shows no such side peaks (Figure 15).

#### DISCUSSION AND CONCLUSIONS

The X-class cells of the area centralis measured in this study, had an average diameter of 0.43 degrees. These diameters are smaller than generally reported (Enroth-Cugell and Robson, 1966; Wiesel, 1960; Rodieck and Stone, 1965b) but agree with some reports (Levick, Cleland and Sanderson, 1973). Although these fields are as small or smaller than those measured by others, they are still significantly larger than those predicted by the C.S.F. to gaussian field theory. Depending on which C.S.F. measurements are taken, the predicted fields would be about 0.10 degrees (Wässle and Creutzfeldt, 1973) or even 0.075 degrees (Berkley and Watkins, 1973). Both of these values are much smaller than the diameters actually found in this or other studies.

Overlap: The area centralis of the cat has about 4000 ganglion cells per square millimeter (Stone, 1965). Approximately one-half of these cells are X-cells (Stone, 1973; Fukuda and Stone, 1974). If these X-cells each have a diameter of 0.43 degrees (0.097 mm) then an average point in the area centralis is encompassed by nearly 15 different X-cell receptive field centers. This extensive overlap could provide the basis for averaging and other types of processing discussed in Part II on Computer Simulation. On the other hand, if the receptive fields were as small as possible, consistent with covering the available space, each field would be about 0.11 degrees wide. Fields of this size are barely adequate to account for some measures of the cats acuity (Wässle and Creutzfeldt, 1973) and actually insufficient to account for other measured acuities (Berkley and Watkins, 1973; Blake et al., 1974) (without further processing, not available because of the lack of overlap). It appears, therefore, that the neural processing in the cat retina is not a strict point-to-point representation but instead involves interaction among large field cells.

Receptive Field Profiles: Knowledge of the detailed receptive field sensitivity profile may be important to the understanding of the neural processing for acuity. However, the attempt to examine these profiles

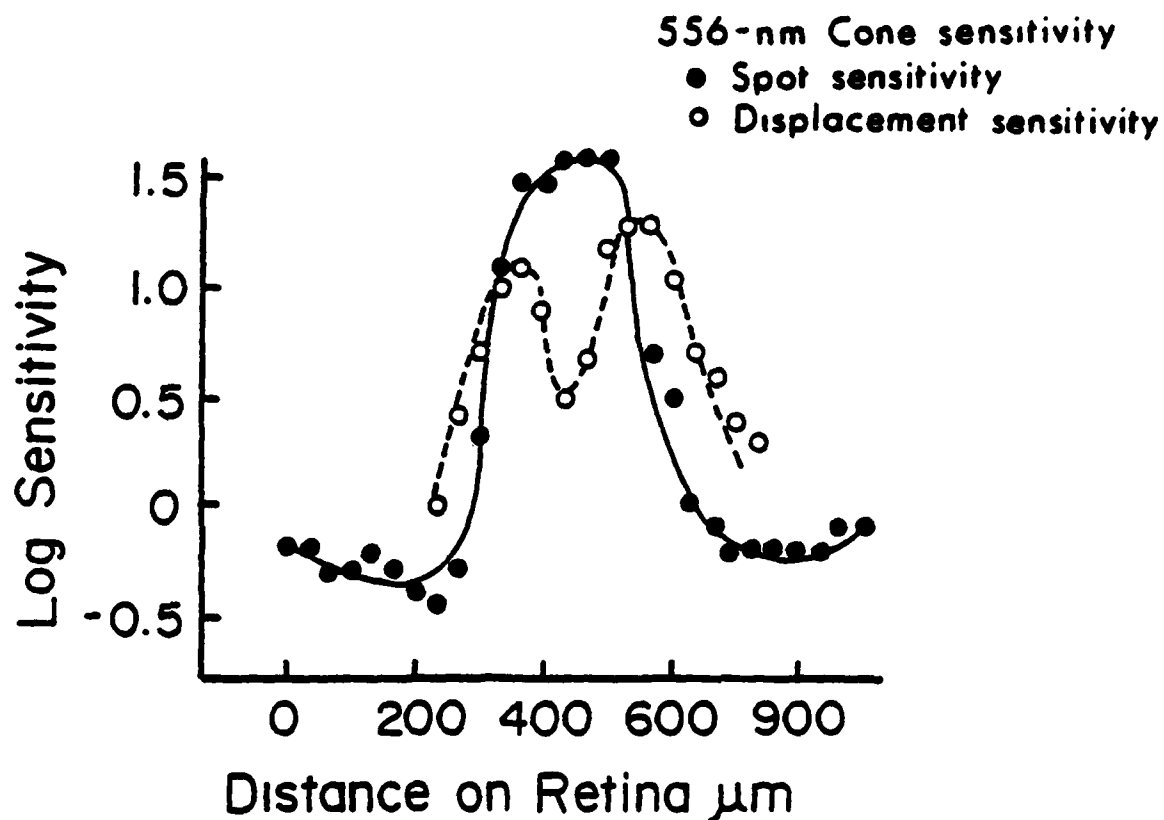


Figure 14: Displacement sensitivity profile for the 556-nm cone. The static spot sensitivity profile and the displacement sensitivity profile were measured as in Figure 13. The displacement sensitivity of the 556-nm cone for this cell is highest at the center surround border. (As in Figure 13, negative sensitivities represent surround OFF responses and should be read as absolute values.) The displacement sensitivity for the 450-nm cone of this cell is shown in Figure 15.

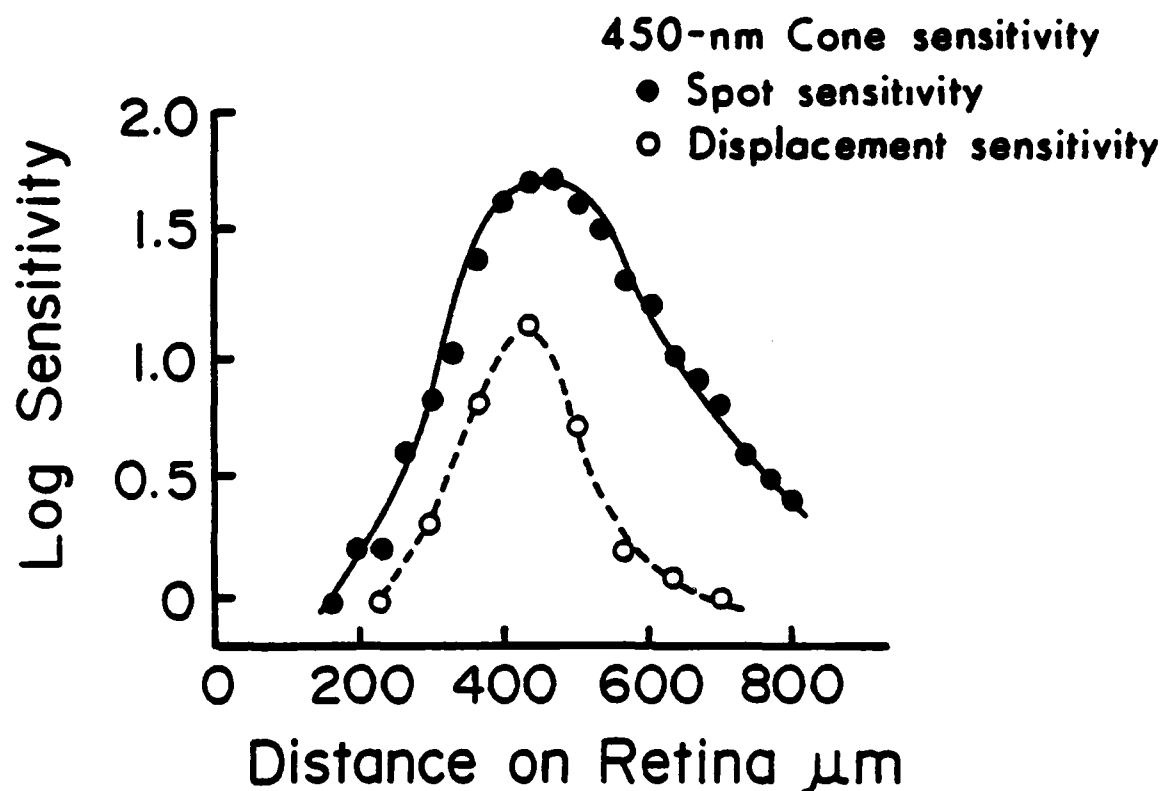


Figure 15: The displacement sensitivity profile of the 450-nm cone. This is the same cell which was shown in Figure 14. The sensitivity measurements were taken under the same conditions as those shown in Figures 13 and 14 except the stimulus was 440 nm light and an orange adapting background was used to bring out the 450-nm cone (background was Wratten #21 equivalent for the rods to  $1.1 \times 10^{10}$  photons  $\text{deg}^{-2} \text{sec}^{-1}$  of 500 nm light). The displacement sensitivity profile for the 450-nm cone shows its highest sensitivity in the same position as the static spot sensitivity profile.



was stymied by the different results found with different methods. At this point it is not possible to determine if either the small exploratory spot method or the Ricco plot method produce an accurate picture of the sensitivity profile since each method has significant drawbacks. The two most important drawbacks are the inherent optical spread of any image and the uncertainties due to possible non-linear summation of light signals within the receptive field.

In the cat the optical spread from a point of white light imaged on the retina has a diameter to  $1/e$  falloff in intensity of almost 10 minutes of arc (Wässle, 1971). Even if a ganglion cell's sensitivity profile were a single receptor, an experimenter exploring with a 6 minute test spot would find a receptive field of at least 15 minutes to the  $1/e$  fall in sensitivity of the test stimulus itself. More accurate measurements of field size can be made for larger receptive fields, but the 15 minute integration (optical spread plus physical spot size) smooths the fine details of any sensitivity profile. The Gaussian-shaped sensitivity profiles generally reported (Cleland and Enroth-Cugell, 1968; DeMonasterio and Gouras, 1975) could in fact be produced by a great variety of actual sensitivity profiles if the stimulus had a 15 minute Gaussian-shaped intensity profile.

Inaccuracies in plotting ganglion cell receptive fields also may arise from the case where receptor output equals a constant multiplied by the log luminance (which is often the case; Barlow, 1972). As an example of such inaccuracies, even assuming that all other stages are linear, suppose that the sensitivity of a particular group of receptors A is twice the sensitivity of a different group B, then the receptor response at the summation point (the input to the ganglion cell) from A and B will be equal when B receives 10 times the illumination of A. This is shown in detail in Table 4. Just this sort of difficulty can arise in Ricco plot experiments. In those types of experiments, sensitivities are compared even though the stimulus luminance levels are very different (in fact necessarily different to compensate for wide differences in stimulus areas). The small exploratory spot method also suffers from this difficulty but to a lesser extent since the luminance levels used do not vary quite so much.

Despite the methodological difficulties it was possible to characterize the center-surround border. In the previous section it was suggested that if the center-surround border is to play an important role in acuity, the border should be sharp. This is exactly what was found. As illustrated in Figures 9, 11, 13 and 14 the cell sensitivity profiles showed their greatest rate of change at the border. This sharpness was found despite the optical blur involved in the small spot which would tend to smooth the sharpness of the border in the measurements.

The abrupt changes in sensitivity at the border were especially well demonstrated by the measurements of displacement sensitivity. The

Table 4  
Variation in Receptor Output as a Function of the Luminance

Receptor Group	A	B
Sensitivity	1	1/2
Stimulus (Units of Light)	10	100
Summing Point Response (R)	$K \log (\text{luminance})$	$K/2 \log (\text{luminance})$
R	$K \log (10)$	$K/2 \log (100)$
R	K	$(K/2) \cdot 2$
R	K	K

Table 4: Inaccuracies in plotting ganglion cell receptive fields may arise from the case where receptor output equals a constant times the log of the luminance. If all other stages are linear, and the sensitivity of a particular group of receptors (A) is twice the sensitivity of a different group (B), then the receptor responses at the summation point (the input to the ganglion cell) from A and B will be equal when B receives 10 times the illumination of A.

small displacements were designed to mimic the displacements caused by the constant natural saccadic movements of the eye. The sensitivity profiles produced with this stimulus showed the greatest sensitivity at the center-surround border. This result serves to emphasize the importance of the center-surround border in at least some circumstances.

The results of the displacement sensitivity measurements made on the blue cone are particularly interesting. The blue cone is generally associated with low acuity (Green, 1968). The usual explanation is that the blue cone receptor density is low. However, the results from the cell illustrated in Figure 15 suggests an alternative or additional neural factor. That is, the ganglion cell organization of the blue cone system lacks sharp borders and perhaps this does not allow for accurate localization by later processing.

The experimental data presented in this report does not provide a complete picture of the cellular mechanisms of acuity vision. As far as it goes, however, the experimental work is consistent with the theoretical conclusions of Part II. The receptive field profile measurements showed a sharp center-surround border which, as the theory suggests could delineate that part of the light pattern contained within the receptive field center.

The receptive field center diameters for X-cells in the area centralis were measured to be about four times larger than the minimum required for coverage of that region. This size provides an overlap of about 15 receptive field centers on any point, and suggests the theory in the introduction that large receptive fields can (and do) mediate higher acuity than small ones.

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